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A NEW SIBLING *PAPILIO* FROM THE ROCKY MOUNTAINS, WITH GENETIC AND BIOLOGICAL NOTES (INSECTA, LEPIDOPTERA)

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Abstract

Papilio gothica (Papilionidae) is described as a new species from montane regions of Colorado and adjacent states. It is a sibling of the lowland Californian *P. zelicaon* and is characterized by subtle color and pattern differences, univoltinism, *Pseudocymopterus montanus* (Umbelliferae) as larval food, and probably distinctive flight behavior. The chromosome number is $n = 30$. Phenotypically *P. gothica* and *P. zelicaon* are nearly alike, but their F_1 hybrids with *P. polyxenes* are unlike. They have different hybrid sex ratios in their crosses with *P. polyxenes, gothica* × *polyxenes* being nearly lethal for the sex of the *polyxenes* parent whereas *zelicaon* × *polyxenes* has more nearly equal sex ratio although deficient in the sex of the *polyxenes* parent. The evolutionary meaning of the principle of phenotypic stability with phyletic divergence is discussed. Phenotypic, biological, and geographic characters are summarized for the North American taxa similar to *gothica,* especially *P. brucei, P. oregonia, P. rudkini,* and *P. hudsonianus.* Photographs are given for all of these as well as *P. gothica* and *P. zelicaon* and hybrids of both crossed with *P. polyxenes* and *P. bairdii.* The foodplant of *P. hudsonianus* in Manitoba is *Zizia* (probably *aurea*) (Umbelliferae). Egg hatchability and embryonic viability are tabulated for *P. gothica, P. zelicaon,* and several hybrid combinations.

The principal purpose of this paper is to validate the name and describe the characteristics of a presently unnamed population, stock from which has been extensively used in my studies of natural and experimental hybridization, caryotypes, foodplant specificity, and population ecology of the *polyxenes–machaon* complex of *Papilio* butterflies. The "new" species has for many years gone under the names *zolicaon* Boisduval, *zelicaon* Lucas, and *brucei* Edwards, but early in my work on this group it became apparent that the abundant, higher altitude, Umbelliferae-feeding entity in Colorado is biologically very different from the low-altitude, Umbelliferae-feeding true *zelicaon* of California and from the mid-altitude, *Artemisia*-feeding true *brucei* of Colorado. My associates and I have informally used the following new name in our research protocols for several years. The formal naming has been delayed in the hope that one or more all-or-none characters would be found by which every dead specimen could be infallibly recognized. Such characters have not yet been discovered, but the name is needed for use in various forthcoming papers and is now designated as follows:

Papilio gothica, species nova

Phenotypically extremely similar to typical Californian *Papilio zelicaon* and some typical Coloradan *P. brucei,* and not always distinguishable at present from these two on any single criterion. In this instance, suitable photographs are truly superior to many words of description, and the accompanying plates will stand in lieu of a routine description of *P. gothica.* Helpful wing characters by which most *gothica* differ from most *zelicaon* or *brucei* are the following:

1. Dorsal ground color sexually dimorphic. Males, Mustard Yellow, Amber-Yellow, or Pinard Yellow (color terms from Ridgway, 1912) [approximately OY-17-11° of Villalobos (1947)]. Females distinctly paler, i.e., usually Straw Yellow of Ridgway. In ground color *P. zelicaon* and *P. brucei* are sexually more monomorphic; both sexes of *P. zelicaon* tend to be similar in color to *gothica* males, and both sexes of *P. brucei* tend to be similar to *gothica* females.

2. Forewing below, in postmedian broad yellow band, with the anterior spot *(pm1* in Fig. 1B) having an outer edge strongly offset from a line drawn through the outer edges of spots 2 through 9; in *zelicaon* and *brucei* the outer edge of the anterior spot tends to be in line with this edge of spots 2 through 9.

3. Forewing below with postmedian spot 2 (*pm2* in Fig. 1B) tending to have its outer edge forming an angle with its caudad edge only slightly greater than 90°; in *zelicaon* and *brucei* this angle is much greater than 90°.

4. Forewing above, near costal edge, usually with two fine

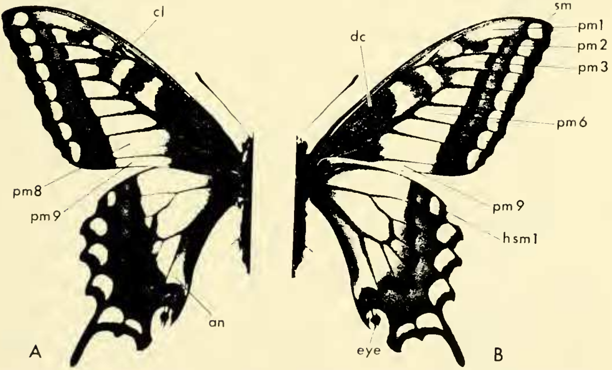


FIG. 1. *Papilio gothica,* illustrating characters used in distinguishing taxa in this complex. A, dorsal surface (upperside); B, ventral surface (underside). Symbols: *pm1* — first pale spot of postmedian row, *pm2* — second pale spot of postmedian row, etc.; *cl* — fine yellow costal lines; *an* — anal marginal cell of hindwing; *dc* — discal cell; *sm* — submarginal row of pale spots of forewing; *hsm1* — first submarginal spot of hindwing; *eye* — "eye" marking of hindwing anal angle.

yellow lines (*c1* in Fig. 1A) opposite end of cell, one anterad and one posterad of the closely parallel veins Sc and R_1; these lines are usually absent in *zelicaon* but frequently are present in *brucei*.

5. Hindwing above has cell Cu_2, near the anal margin (*an* in Fig. 1A), with basal dark color usually extending far distad of origin of vein Cu_2 from cell; this dark area tends to be greatly reduced in *zelicaon* males and in both sexes of *brucei*.

6. Forewing below with spots of submarginal yellow row (*sm* in Fig. 1B) large and tending toward fusion; in *zelicaon* these spots tend to be smaller and to be separated clearly by blackening of the veins crossing this row, and in *brucei* these spots are even larger and more fused than in *gothica*.

7. Forewing tends to be slightly more rounded at the apex and to form a more acute angle between anal and outer margins than in *zelicaon; brucei* tends to have this angle much more obtuse than *gothica* or *zelicaon*.

8. Forewing below with basal half of discal cell (*dc* in Fig. 1B) entirely black (extremely rarely there is yellow streaking, perhaps an indicator of introgressive hybridization with *brucei*); *zelicaon* is like *gothica*, but *brucei* usually has extensive yellow scaling in this area (see Fig. 35).

9. Hindwing below with eyespot at anal angle (*eye* in Fig. 1B) tending to have the black "pupil" moderately large, rounded, and thinner than the orange area just cephalad; in *zelicaon* this "pupil" is even larger and tends to equal or exceed the thickness of the orange area, whereas in *brucei* the "pupil" is usually very thin, transverse, and less than half the thickness of the orange area. This character often shows strong asymmetry, with one hindwing having a smaller "pupil" than the other.

10. Hindwing below with the first spot of the submarginal yellow row (*hsm1* in Fig. 1B) tending to be somewhat broader than in *zelicaon* and much narrower than in *brucei;* on the upperside this spot tends to obsolescence in many *zelicaon*.

11. Hindwing tail tends to be slightly shorter and slenderer than that of *zelicaon;* that of *brucei* tends to be longer and slenderer than that of *gothica* or *zelicaon*.

The most reliable characters for distinguishing adults of montane Coloradan *gothica* from lowland coastal Californian *zelicaon* appear to be numbers 2, 3, 4, and 5.

In addition to these wing characters, it should be noted that in *P. gothica* the abdomen has the venter usually plain black and the lateral yellow line slender; *zelicaon* resembles *gothica,* but on females the lateral yellow stripe is wider, and *brucei* has much more extensive yellow on the sides and often on the entire venter.

A preliminary inspection of the several available preserved larvae and pupae has not revealed readily quantifiable taxonomic distinctions. However, there is an interesting gene-frequency difference in larval spot color (see below, under Genetical Studies).

The chromosome complement of *P. gothica,* reported under temporary terminology as *"Papilio 'brucei'"* by Maeki and Remington (1960), shows n = 30, without the m-chromosome reported from *P. polyxenes.* Two males from the supposed *zelicaon* population from the Cascade Mountains of Okanogan County, Washington, also had n = 30 and lacked the m-chromosome (Remington & Maeki, unpublished). Testes of various lowland Californian *zelicaon* have been collected but not yet sectioned.

TYPE SPECIMENS

Although there is no doubt that *P. gothica* is widely distributed in the Rocky Mountain region and probably in some areas farther west (see below), I am limiting my type series to specimens from the Colorado mountains, as follows:

HOLOTYPE MALE (Figs. 2 and 4): Gothic, 9500′, Gunnison Co., Colorado, 14 June 1956, leg. Eric E. Remington; in Peabody Museum of Natural History.

REPRESENTATIVE FEMALE PARATYPE (Figs. 3 and 5): Gothic, 9500′, Gunnison Co., Colorado, 28 June 1960, leg. Eric E. Remington; in Peabody Museum of Natural History.

PARATYPES (two pairs shown in Figs. 6-9 and 14-17). Forty adult males, twelve adult females, four larvae, and sixty-two pupae, all from Colorado. Gothic, Gunnison Co., males: 13 June 1956 (C. L. Remington), 14 and 27 June 1956 (E. E. Remington), 6 July 1956 (R. W. Pease Jr.), 11-12 July 1957 (R. W. Pease

Jr.), 28 June 1959 (E. E. Remington & B. Baker), 12 July 1959 (R. W. Pease Jr.), 28 June 1960 (E. E. Remington) (CLR testes #740), 13 July 1960 (*ex pupa,* bred *ab ovo,* CLR testes #629), two 1 July 1961 (E. E. Remington); females: 10-14 July 1957 (S. A. Ae), 30 July 1957 (E. E. Remington), 1 Aug. 1957 (S. A. Ae), 28 and 29 June 1960 (E. E. Remington), 26 June 1961 (B. Baker). East of Copper Lake, 10,500′, above Gothic, Gunnison Co., 4 July 1960 (E. E. Remington), female. Virginia Basin, 12,500′, above Gothic, Gunnison Co., 20 July 1956 (R. W. Pease Jr.), male. Cumberland Pass, 12,600′, Gunnison Co.: 28 July 1955 (C. L. Remington), two males (fathers of CLR hybrid broods #10 and #12), 12 July 1967 (C. G. Oliver), male. Mt. Bellview, 12,500′, north of Gothic, Gunnison Co., 4 July 1956 (R. W. Pease Jr.), 6 males. Elkton townsite, 10,000′, Gunnison Co., 12 July 1959 (C. L. Remington), male. Eldora, 8800′, Boulder Co.: 16 June 1933 (P. S. & C. L. Remington), female; 28 June 1937 (P. S. & C. L. Remington), male; 30 June 1937 (P. S. & C. L. Remington), 3 males and 1 female; 3 July 1937 (P. S. & C. L. Remington), 3 males; 23 July 1949 (C. L. Remington), 2 males. Mt. Audubon, 11,000′, Boulder Co., 26 July 1949 (C. L. Remington), male. Arapaho Pass, 11,900′, Boulder Co., 17 July 1937 (P. S. & C. L. Remington), male. Boulder Canyon, 8000′, Boulder Co., 19 June 1933 (P. S. & C. L. Remington), male. 5 mi. N. of Eldora, 11,500′, Boulder Co., 10 July 1947 (P. S. Remington), female. Tolland, 8700′, Gilpin Co., 2 July 1937 (P. S. & C. L. Remington), 2 females. 3 mi. N. of Rabbit Ears Pass, 10,000′-10,600′, Routt Co., 15 and 16 July 1956 (F. & P. Rindge), 6 males. The 6 Routt Co. males are in the American Museum of Natural History, and the 1967 Cumberland Pass male is in the collection of Charles G. Oliver. The remaining 33 males and 11 females are at present in the Peabody Museum of Natural History and my own genetical collection.

Also designated as paratypes are four preserved larvae taken at Gothic (three, 6 Aug. 1956, F_1 of wild female, leg. E. E. Remington & S. A. Ae; one, found on Umbelliferae, preserved 18 July 1955, leg. R. W. Pease Jr.) and 42 living, diapausing pupae reared from Oliver female #1 collected wild at Taylor Park, 9400′, Gunnison Co., 2 July 1967, by C. G. Oliver.

NOMENCLATURE

The new entity is named for Gothic, a locale at 9500′ elevation in the West Elk Range of the Colorado Rocky Mountains. Gothic was originally founded as a town during the silver mining boom of the late 1870's and early 1880's but was soon abandoned. In the early 1930's the Rocky Mountain Biological Laboratory was developed on the site and has been an unexcelled center for research in the biology of montane organisms by many investigators. Much of my experimental and field work with the evolutionary genetics of Lepidoptera, including *Papilio gothica,* has been carried out there, hence the appropriateness of the name. The name *gothica* as used here is a substantive, not an adjective.

It is curious that no name was available in the literature that might be applied to this very wide-ranging, handsome, and often abundant butterfly of the Rocky Mountain region, but I am certain that this is so. The types of Lucas' *zelicaon* (which I examined in the Muséum National d'Histoire Naturelle in Paris in 1958) and Boisduval's *zolicaon* were collected solely in California, by P. J. M. Lorquin. *P. coloro* Wright (1905), from California deserts, is probably *zelicaon* but may be a hybrid *zelicaon* × *rudkini.* Fischer's (1908) "impunctata", "melanotaenia", and "formosa" were named without locality designations as aberrations of *zelicaon;* these are in fact trivial minority forms in *zelicaon* (and perhaps in *gothica*) populations, and their names are nomenclaturally unavailable at the species—subspecies level. Gunder (1928) named "mcdunnoughi" as a "transition form", and it, too, clearly applies to a minority form in populations and is unavailable as the name for *gothica,* although the holotype is from Waterton Lakes, Alberta, and may be *gothica;* Gunder's paratypes of this aberration are from Wyoming, "Colorado", and California. The names *dodi* McDunnough and *avinoffi* F. & R. Chermock apply to the *hudsonianus* complex (see below), not to *gothica.* I have proven *P. nitra* Edwards (the types of which I have examined at the Carnegie Museum) to be an interspecific hybrid, and this name is unavailable for any species or subspecies. Edwards' true *P. brucei,* the status of which is discussed below, is not the taxon here named *gothica,* although the name *brucei* has recently been used for it with explicit reservations (Remington, 1958; Maeki & Remington, 1960; Ae, 1965). The specimen figured without locality notation by Brown (1956) as "*zelicaon*" was meant to represent what I now call *gothica*, but if it is *gothica*, it is highly atypical in my characters 2, 3, 4, 5, and 8.

STATUS AND RELATIONSHIPS

Although I am formally erecting *Papilio gothica* as a nomenclatural entity with full species status, I consider this a tentative placement. It needs to be tested by thorough backcross studies of hybrid fertility and developmental viability and by analysis of interactions in localities where some sympatry exists. My assistants and I have successfully crossed *gothica* and *zelicaon* eight times, but the status of *gothica* has been a relatively narrow aspect of my broad experimental study of evolutionary processes in the *polyxenes–machaon* group, and by chance I have not yet had the ideal congruence of the appropriate livestock and seasonal breeding facilities that would have allowed me to complete the *gothica–zelicaon* tests. Furthermore, I have not been able to do any field studies in sites of sympatry.

In considering 1) the evidence of normally concealed genetic differences between *gothica* and *zelicaon*, even in wing characters, that are revealed in their separate hybrids with *polyxenes* tester stocks, 2) the difference in sex-ratio distortion also shown in test-crosses with *polyxenes*, and 3) their probably profound biological differences, I have only a little hesitation in placing them as separate species. In all groups of animals, most pairs of largely allopatric, closely related taxa that are routinely treated as separate species are even less well known genetically than these two *Papilio*.

There are several other North American entities in the *polyxenes–machaon* complex that have the broad yellow wing-band and the yellow-and-black-striped abdomen and therefore superficially resemble *P. gothica* and *P. zelicaon*. Most of these are shown, along with some of presently unknown status, in Figs. 24-29 and 32-37.

Papilio oregonia Edwards and *P. brucei* Edwards appear to me to be subspecies of *P. bairdii* Edwards. Ever since the brilliant work of Edwards and Bruce in the late nineteenth century, this has been a widely accepted allocation. However, the nature of natural hybridization (a rather narrow zone of polymorphism rather than clinal intermediacy) hints that *bairdii* had attained the species level prior to sympatry with *brucei*. All three taxa seem to be restricted to *Artemisia dracunculoides* (Compositae) as their larval foodplant and to be multivoltine throughout their range. All are unusually variable, perhaps due substantially to introgression between the three and to a lesser degree to hybridization with all the other members of the *polyxenes–machaon* complex with which they have some present or recent sympatry. Since *bairdii* does not resemble *gothica*, its dead-specimen characters need not be considered here. *P. oregonia* (Figs. 26 and 34) is easily distinguishable in having extensive yellow coloration in the forewing cell below, a tendency for a peppering of yellow scales over the dark areas of the upperside of both wings, a marked caudad displacement of the black "pupil" in the hindwing anal eyespot (rarely, the "pupil" is centered as in *zelicaon*). *P. brucei* (Figs. 27 and 35) is a useful name for the *oregonia*-like populations of Colorado, Utah, Arizona, and possibly the northern Rocky Mountain region. It has less yellow scaling in the forewing cell than does *oregonia* (sometimes no yellow at all), and the black "pupil" of its eyespot tends to be less displaced than in *oregonia*. Differences between *brucei* and *gothica* or *zelicaon* are noted in the diagnosis for *gothica* above.

Papilio rudkini Comstock appears to be a distinct species, although it was originally named as a race of *bairdii*. It seems to be more closely related to *P. zelicaon* than to the *bairdii* complex. Its larvae are said to be restricted to *Thamnosma montana* (Rutaceae), and it is multivoltine. It is sympatric with *P. zelicaon* in some desert regions of southern California, with *P. oregonia* in western Nevada and perhaps eastern California and southwestern Oregon, and possibly with *P. brucei* and even *P. gothica* in Utah and northern Arizona. *P. rudkini* (Figs. 24, 25, 32, 33) differs from *gothica* and *zelicaon* in having the second postmedian spot of the forewing below (see *pm2* in Fig. 1B) with its outer edge arrowhead-shaped, the black spot in *pm2* very large, the caudad yellow bar of the postmedian row (*pm9* in Fig. 1A) with a prominent *caudad* inward extension especially in males, the forewing submarginal spots (*sm* in Fig. 1B) much more discrete and rounded, the anal-edge cell of the forewing above (*an* in Fig. 1A) with the basal black more restricted, the hindwing above with much less postmedian blue color in males, the tail usually longer, the forewing slenderer and forming a more acute angle between the costal and outer margins, and a tendency for the yellow ground color of the male to be more ochreous and that of the female more pale-yellow(i.e., more sexual dimorphism in ground-color). Two supposed forms of *rudkini* ("comstocki" and "clarki") do not closely resemble *gothica* and need not be considered here. Their genetical status is now being investigated by Fred T. Thorne.

Papilio hudsonianus Clark and similar entities from the Dakota Badlands, Nebraska, northeastern Wyoming, Manitoba, Saskatchewan, Alberta, and Montana have been associated with the European and Alaskan *P. machaon* Linné (e.g., Clark, 1932). There is as yet little biological or genetic evidence for this association, and I am inclined to doubt its correctness (Remington, 1956). These populations resemble *gothica* and *zelicaon* but are, in my opinion, specifically distinct; they seem to be multivoltine and to feed on Umbelliferae. We found eggs and larvae on *Zizia* sp. (probably *aurea*) at Riding Mountain, Manitoba. All the many specimens I have seen from North Dakota, Nebraska, and Manitoba belong to this group. Neither true *gothica* nor *zelicaon* seems to occur in those areas, although there is a small, univoltine, *gothica*-like *Papilio* in the higher elevations of the Black Hills of South Dakota. The *hudsonianus*-like specimens tend to have some yellow scales in the forewing cell below and to have the eyespot "pupil" displaced caudad, much as in *brucei,* but the forewing tends to be longer, narrower, and more acute-tipped than in *brucei.* In fact, these specimens resemble *brucei* in so many subtle characters that they might be considered conspecific if they were not regularly associated with Umbelliferae. Should *Artemisia*-feeding larvae also be found in this northern Plains region (where *A. dracunculoides* is not uncommon), this would support my suspicion from dead-specimen analyses that *brucei* and the *hudsonianus* type have recently become widely sympatric and are hybridizing relatively freely. This is a region in which extensive and probably recent natural hybridization is now known in many genera of plants, vertebrates, and insects (see Remington, 1968).

As Clarke and Sheppard (1955) noted, this group is exceptionally suitable for the study of processes of speciation. But it is much too complicated for grand conclusions based on scanty breeding experiments or on specimen samples from a few distant, randomly-chosen localities. Not surprisingly, recent experimental and field studies have tended to support the tentative taxonomic conclusions of workers who were widely acquainted with these butterflies in the field as well as from extensive specimen material (e.g., Edwards, 1895, and Bauer, 1955). Unfortunately, foreign and some North American authors who have attempted, without such acquaintance, to deal with the relationships and status of these and other North American members of the *polyxenes–machaon* complex have been wide of the mark in their conclusions (e.g., Rothschild & Jordan, 1906, Clark, 1936, Eller, 1936, Clarke & Sheppard, 1953 *et seq.*).

Throughout this paper I have used binomina without necessarily implying full species status. For example, I consider *Papilio brucei* to be a definite deme, probably conspecific with *P. oregonia* and possibly with *P. bairdii. Papilio avinoffi* is surely conspecific with *P. hudsonianus* and possibly with *P. machaon.* Where I do not wish at this time to specify the hierarchical status of a taxon, it is most convenient to refer to it with a binomen.

GEOGRAPHY

Populations with the *gothica–zelicaon* facies are known from New Mexico, Arizona, Colorado, Utah, Nevada, South Dakota, Wyoming, Montana, Idaho, Alberta, British Columbia, Washington, Oregon, California, and Baja California. As will be discussed below, each deme is at present best allocated to either *gothica* or *zelicaon* after hybridization against *polyxenes* tester stocks and after the assay of voltinism, of oviposition plants, and probably of flight behavior. Most of the dead-specimen records from this wide geographic range are not now placeable with certainty because they are not associated with enough data. I am confidently allocating the specimens from the higher mountains of New Mexico, Colorado, and Wyoming to *P. gothica* and all specimens from the Pacific Slope lowlands of California south of San Francisco Bay to *P. zelicaon. P. zelicaon* also occurs farther to the north and east, but I do not know how far. I suspect, from a study of wing characters, the montane populations of Montana, Idaho, Utah, Alberta, and eastern British Columbia are *gothica*. The two females from the Ruby Mountains of eastern Nevada that I have examined are like *gothica* in wing characters (see Figs. 23 and 31); the few from Reno are *zelicaon* or have indecisive character states. The populations of the high Sierras and of the Coast Range of northwestern California and western Oregon resemble *gothica* somewhat more than *zelicaon*. I have examined long series from low elevations of Okanogan County, Washington, and Vancouver Island, British Columbia, and these seem to be closest to *zelicaon;* the F_1 hybrids between eastern *polyxenes* and the Okanogan County deme definitely have the phenotype of *polyxenes* × California *zelicaon*. (See discussion, below, of this hybrid difference.) Partial sympatry between the two is to be sought at mountain—lowland contacts in central and eastern California, western Nevada, Oregon, southern and western Idaho, western Washington, and eastern Montana. There may be a cline connecting *gothica* and *zelicaon* in this region, but my skimpy evidence suggests that there is interspecific hybridization rather than clinal intermediacy.

BIOLOGY

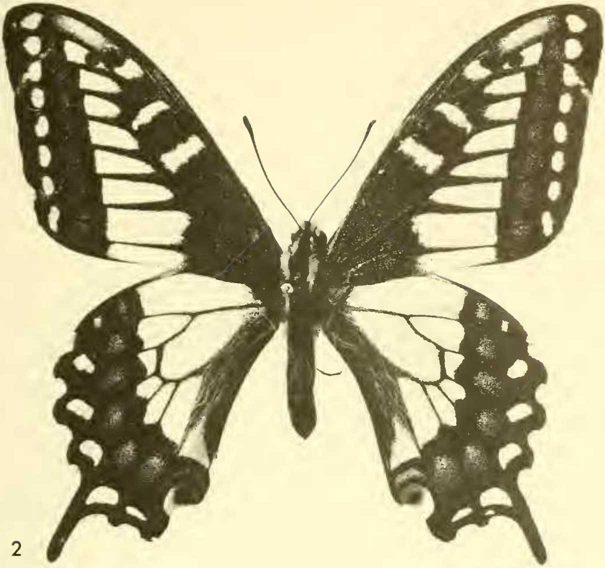
Papilio gothica in Colorado is principally a montane taxon, occurring moderately abundantly from about 6000 feet above sea level, up to tree-line, in most or all of the mountain ranges in the state. The tree-limit is at about 11,400 feet in the Front Range in Boulder County (Marr, 1961) and slightly higher in the Elk Range in Gunnison County (Langenheim, 1962), the two areas where I have worked most intensively with *P. gothica*. Although there is no evidence that *gothica* is a permanent resident above the tree-line, males are commonly found exhibiting hilltopping behavior around summits above tree-line, even as high as 14,000 feet. Typical *P. gothica* probably does not normally occur as a resident out on the lowlands to the east of the Front Range or to the west between the mountain ranges. There is a phenotypically slightly different population at the plains–mountain interface at the eastern edge of the Front Range which may prove to have major biological distinctions from *gothica*. Without further field and breeding study it would be premature to name

PLATE SECTION

FIG. 2. *Papilio gothica* Remington, HOLOTYPE ♂. Gothic, 9500′, Gunnison Co., Colorado, 14 June 1956, leg. E. E. Remington.

FIG. 3. *Papilio gothica*, representative PARATYPE ♀. Gothic, 9500′, Gunnison Co., Colorado, 28 June 1960, leg. E. E. Remington.

Dorsal surface; for venter see Figs. 4 and 5. × 1.5



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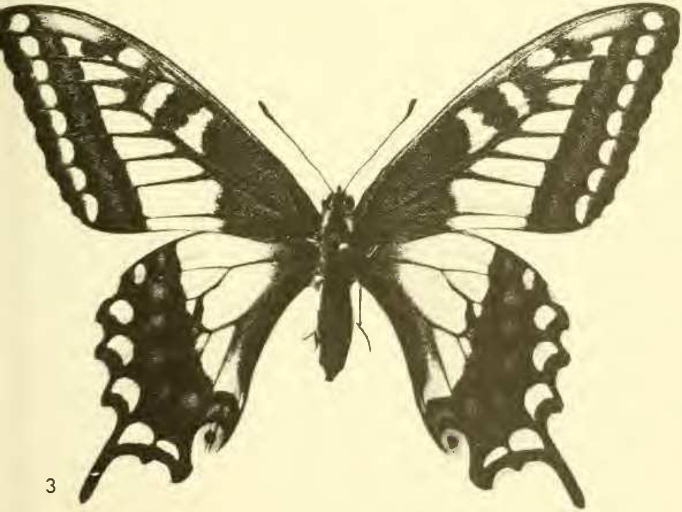

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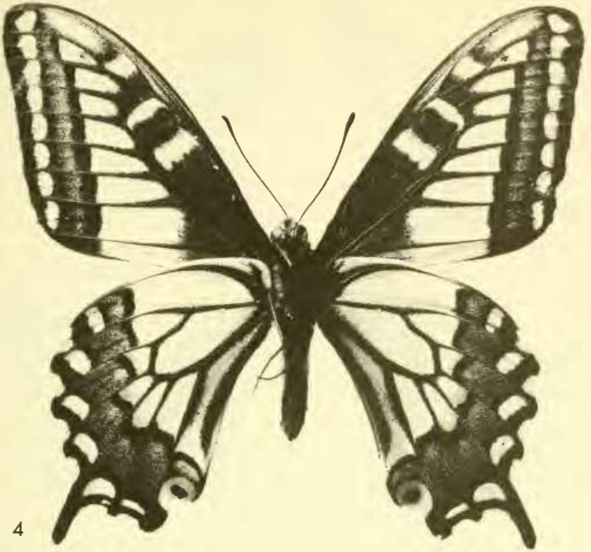
FIG. 4. *Papilio gothica*, HOLOTYPE ♂.

FIG. 5. *Papilio gothica*, representative PARATYPE ♀.

Ventral surface of specimens shown in Figs. 2 and 3.



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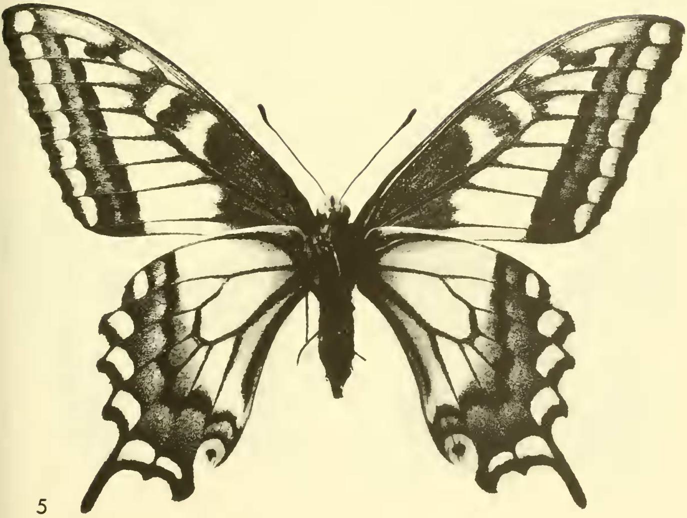

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FIG. 6. *Papilio gothica* Remington, PARATYPE ♂, Gothic, 9500′, Gunnison Co., Colorado, 6 July 1956, leg. R. W. Pease Jr.

FIG. 7. *Papilio gothica*, PARATYPE ♀, Gothic, 9500′, Gunnison Co., Colorado, 28 June 1960, leg. E. E. Remington.

FIG. 8. *Papilio gothica*, PARATYPE ♂, Mt. Audubon, 11,000′, Boulder Co., Colorado, 26 July 1949, leg. C. L. Remington.

FIG. 9. *Papilio gothica*, PARATYPE ♀, Eldora, 8800′, Boulder Co., Colorado, 30 June 1937, leg. P. S. & C. L. Remington.

FIG. 10. *Papilio zelicaon* Lucas, ♂, Berkeley, California, 22 June 1932.

FIG. 11. *Papilio zelicaon*, ♀, Berkeley, California, 25 May 1932.

FIG. 12. *Papilio zelicaon*, ♂, La Jolla, San Diego Co., California, 27 Aug. 1943, leg. D. Starrett.

FIG. 13. *Papilio zelicaon*, ♀, Summerland, Santa Barbara Co., California, 4 May 1931, leg. C. W. Kirkwood.

Dorsal surface; for venters see Figs. 14-21. × .75

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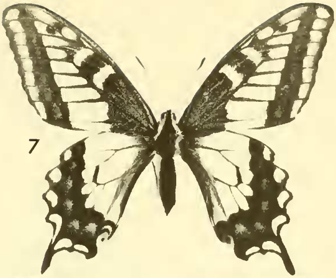

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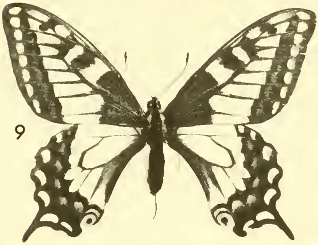

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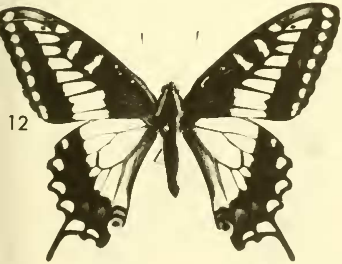

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FIG. 14. *Papilio gothica*, PARATYPE ♂.

FIG. 15. *Papilio gothica*, PARATYPE ♀.

FIG. 16. *Papilio gothica*, PARATYPE ♂.

FIG. 17. *Papilio gothica*, PARATYPE ♀.

FIG. 18. *Papilio zelicaon*, ♂.

FIG. 19. *Papilio zelicaon*, ♀.

FIG. 20. *Papilio zelicaon*, ♂.

FIG. 21. *Papilio zelicaon*, ♀.

Ventral surface of specimens shown in Figs. 6-13.


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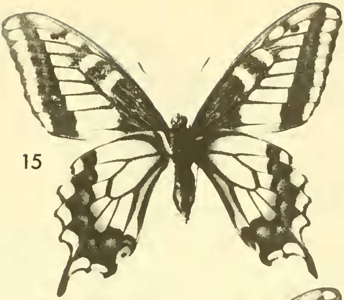
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FIG. 22. *Papilio* (*zelicaon*?), ♂, Pateros, Okanogan Co., Washington, 1 May 1935, leg. A. Anderson.

FIG. 23. *Papilio* (*gothica*?), ♀, Lamoille Canyon, Ruby Mts., Elko Co., Nevada, 28 June 1959, leg. T. W. Davies.

FIG. 24. *Papilio rudkini* Comstock, ♂, Mexican Well, Ivanpah Mts., San Bernardino Co., California, 1-2 Sept. 1934, leg. C. N. Rudkin.

FIG. 25. *Papilio rudkini*, ♀, Mexican Well, el. 4800′, Ivanpah Mts., San Bernardino Co., California, larva on *Thamnosma montana* 17 Sept. 1934, eclosed 28 Feb. 1936, leg. C. Henne.

FIG. 26. *Papilio oregonia* Edwards, ♀, Brewster, Okanogan Co., Washington, 2 Aug. 1952, leg. J. C. Hopfinger.

FIG. 27. *Papilio brucei* Edwards, ♂, Glenwood Springs, Garfield Co., Colorado, 18 July 1961, leg. O. R. Taylor Jr.

FIG. 28. *Papilio avinoffi* Chermock & Chermock, ♀, F_1 of C.L.R. cross #83 (mother and father reared from ova found on *Zizia*, Riding Mt., Manitoba, leg. C. L. Remington & R. W. Pease Jr.), eclosed 30 June — 2 July 1956.

FIG. 29. *Papilio hudsonianus* — *avinoffi* group, ♂, Killdeer Mts., Dunn Co., North Dakota, 23 May 1964, leg. J. Oberfoell.

Dorsal surface; for venters see Figs. 30-37. × .72


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FIG. 30. *Papilio* (*zelicaon*?), ♂.

FIG. 31. *Papilio* (*gothica*?), ♀.

FIG. 32. *Papilio rudkini*, ♂.

FIG. 33. *Papilio rudkini*, ♀.

FIG. 34. *Papilio oregonia*, ♀.

FIG. 35. *Papilio brucei*, ♂.

FIG. 36. *Papilio avinoffi*, ♀.

FIG. 37. *Papilio hudsonianus — avinoffi* group, ♂.

Ventral surface of specimens shown in Figs. 22-29.


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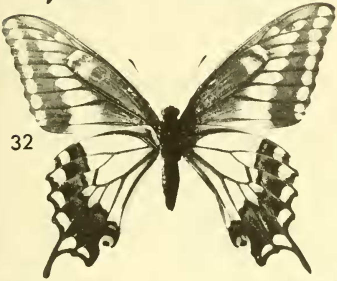
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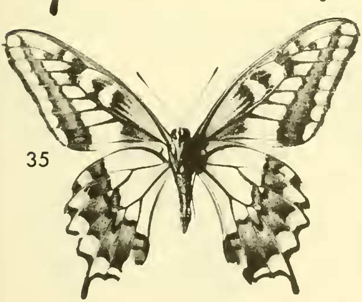
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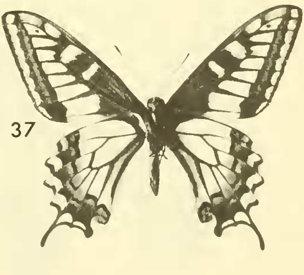
37

FIG. 38. *Papilio* F_1 hybrid ♀ *polyxenes* × ♂ *gothica* (Remington brood #10), ♂, eclosed 14 May 1956, bred C. L. Remington & R. W. Pease Jr.; usual phenotype for this parentage.

FIG. 39. *Papilio* F_1 hybrid ♀ *polyxenes* × ♂ *gothica* (brood #10), ♂, eclosed 19 May 1956; chosen as showing wider hindwing median yellow band than usual for this parentage.

FIG. 40. *Papilio* F_1 hybrid ♀ *polyxenes* × ♂ *zelicaon* (Remington brood #115), ♂, eclosed 24 July 1956, bred C. L. Remington & R. W. Pease Jr.; chosen as showing narrower hindwing median yellow band than usual for this parentage.

FIG. 41. *Papilio* F_1 hybrid ♀ *polyxenes* × ♂ *zelicaon* (brood #115), ♂, eclosed 23 July 1956; usual phenotype.

FIG. 42. *Papilio* F_1 hybrid ♀ *gothica* × ♂ *bairdii* (Remington brood #337A), ♂, eclosed 14 May 1958, bred C. L. Remington & R. W. Pease Jr.

FIG. 43. *Papilio* F_1 hybrid ♀ *gothica* × ♂ *bairdii* (brood #337A), ♂, eclosed 23-29 Aug. 1957.

FIG. 44. *Papilio* F_1 hybrid ♀ *zelicaon* × ♂ *bairdii* (Remington brood #452), ♂, eclosed 5 June 1958, bred R. W. Pease Jr.

FIG. 45. *Papilio* F_1 ♀ *zelicaon* × ♂ *bairdii* (brood #452), ♂, eclosed 4 June 1958.

Dorsal surface (ventral surface not illustrated). × .68


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this population, but I am excluding all specimens of it from the type series of *gothica*. I have examined a large sample of this plains-edge deme collected at the mouth of Jarre Canyon in Douglas County, Colorado, and I have inspected other specimens from similar biotopes in Wyoming, Montana, the Dakotas, and Alberta. I have noted (Remington, 1958, 1968) that typical *gothica* is presently hybridizing with the eastern *Papilio polyxenes*. I now know that the plains-edge deme is also crossing with *P. polyxenes*. Surprisingly, the two kinds of hybrids are phenotypically dissimilar, and this is the principal evidence that inclines me to the view that there are two *gothica*-like species or semispecies in Colorado. Because no consistent phenotypic differences have been found between typical *gothica* and the plains-edge deme, it is not at present possible to assay natural interbreeding between these two. Similarly, I cannot with certainty recognize backcross or even F_1 hybrids between *gothica* and *brucei*, so I do not yet know how extensively these two are hybridizing at their few known contact points; Edwards' (1895) report of the rearing of occasional *"zelicaon"*-like specimens from *brucei–bairdii* broods from Glenwood Springs, Colorado, perhaps indicates hybridization there with *gothica*.

Typical *P. gothica* is crisply univoltine in Colorado and probably throughout its range. Not only do the pupae normally require chilling or long aging to break diapause, but larval development in the laboratory is significantly slower than that of the several multivoltine members of the *polyxenes–machaon* group that I have reared. Typical *P. zelicaon* has several generations per year, and fresh adults are present in parts of coastal southern California almost every month of the year (see, e.g., Comstock, 1927). *P. brucei* is at least bivoltine at Glenwood Springs. It is not known whether there is a second generation of the plains-edge deme at Jarre Canyon, but its presumed counterpart in Wyoming and Montana has at least two generations per year.

In flight *P. gothica* seems to be swifter and more elusive than typical *P. zelicaon*. An objective quantitative assay of flight behavior would be difficult to make, but my subjective impression of differences comes from the three times when I have successively observed *gothica* and *zelicaon* closely in the field during the same or consecutive years.

There also appears to be a substantial difference in foodplant choice by ovipositing females. In coastal California, the principal foodplant of *P. zelicaon* is the introduced weed *Foeniculum vulgare* (see, e.g., Coolidge, 1924; Comstock, 1927), and it readily oviposits on cultivated Umbelliferae and even the rutaceous genus *Citrus*. *P. gothica*, however, seems to reject weedy and cultivated umbellifers. Several times, at the proper season, I have searched with no success for eggs and larvae on large beds of carrot *(Daucus carota)* and parsley *(Petroselinum crispum)* in kitchen gardens in Crested Butte, near Gothic; *P. gothica* is present at Crested Butte. Similarly, I have fruitlessly examined hundreds of Queen-Anne's-Lace (wild *D. carota*) in the mountains of Boulder County, in localities where *gothica* is abundant and at a season when larvae were to be expected. The failure is a true indicator of *gothica* oviposition choice rather than any lack of experience in my finding eggs and larvae, since I have had no difficulty in finding many hundreds of wild eggs, small larvae, and mature larvae of the closely related *P. polyxenes* on wild and cultivated *D. carota* and cultivated *Petroselinum* and *Apium*, as well as other hundreds, in total, of the related *P. brevicauda, P. kahli, P. zelicaon, P. bairdii,* and *P. gothica* itself on various native species of Umbelliferae and *Artemisia dracunculoides*. My assistants and I have recorded the foodplants of five wild larvae of *P. gothica,* all taken at Gothic; all were on *Pseudocymopterus montanus* (A. Gray) Coulter & Rose: early July (2) and 25 July 1956; 13 and 20 August 1961. During the course of my genetical studies of these *Papilio* species we have brought into the laboratory from the vicinity of the Gothic Meadow several thousand fresh plants of *Ligusticum porteri* Coulter & Rose and *Oxypolis fendleri* (A. Gray) A. Heller, and hundreds of *P. montanus* and *Heracleum lanatum* Michx., for use as larval food. All are satisfactory laboratory foods for *gothica,* and all are abundant where females fly, but careful examination of all of these plants has revealed larvae or eggs only on *P. montanus*. *Pseudocymopterus* is surely the preferred wild host of *gothica* in Colorado.

Another difference in ovipositional behavior is suggested by my observations in Colorado and coastal California. All of our wild eggs and first instar larvae of *P. gothica* have been found on the flower umbels, although foliage was conspicuous and abundant.

Further, without identifying the specific releasers, we have consistently gotten much larger egg production from confined females given umbels than those given leaves as an oviposition substrate. Thus, it appears that *gothica* prefers to oviposit on the flower head. In my studies of *zelicaon* at Santa Barbara and on Santa Cruz Island, in California, I have found large numbers of eggs and first instar larvae on foliage of *Foeniculum,* usually on very young shoots; far fewer have been on umbels, except when the plants are mature and tall and have few or no young leaf shoots. Thus, it appears that *zelicaon* chooses to oviposit on both the foliage and the flower head, perhaps preferring the leaves. Among related species, my rather extensive observations show that *P. kahli* in Manitoba chooses the flower heads of *Zizia, P. brevicauda* (or its hybrid with *polyxenes*) in New Brunswick chooses flower heads of *Ligusticum,* and *P. polyxenes* in Connecticut and Missouri chooses flower heads of wild *Daucus;* in the absence of flowers, I have found that wild females of *polyxenes* oviposit readily on foliage of *Petroselinum, Apium,* and garden *Daucus.*

GENETICAL STUDIES

The wing characters of *Papilio gothica* and *P. zelicaon* being nearly identical, it was not surprising that F_1 hybrids between them do not show distinctive wing characters of their own. Unexpectedly, however, when *gothica* and *zelicaon* were crossed with a single tester species, *P. polyxenes,* the F_1 hybrids of *polyxenes* × *gothica* proved to be easily distinguishable from *polyxenes* × *zelicaon.* A similar set of crosses using *P. bairdii* as the tester likewise revealed phenotypic differences between F_1 of *gothica* × *bairdii* and *zelicaon* × *bairdii.* These and other tester crosses also showed that *gothica* parentage produces a hybrid sex ratio significantly different from that from *zelicaon* parentage. Thus, it is clear that the extreme similarity in dead-specimen characters conceals important genetic divergence between *P. gothica* and *P. zelicaon.* Some details follow.

F_1 hybrids of *P. polyxenes* ♀ × *P. gothica* ♂ (Figs. 38 and 39) have all the yellow markings more reduced on the upperside of the wings and on the abdominal sides than do the F_1 hybrids of *P. polyxenes* ♀ × *P. zelicaon* ♂ (Figs. 40 and 41). Also, these yellow wing markings are paler with *gothica* parentage and more ochreous from *zelicaon* parentage. For a brief account of the genetics of the broad-banded wing and striped abdomen of *gothica* and the dark wing and spotted abdomen of *polyxenes*, see my earlier paper (Remington, 1958).

When *bairdii* is the tester, both combinations show wider yellow postmedian bands than with *polyxenes*, but again the band is narrower in F_1 of *gothica* ♀ × *bairdii* ♂ (Figs. 42 and 43) than in F_1 of *zelicaon* ♀ × *bairdii* ♂ (Figs. 44 and 45), and the lateral spotting of the abdomen is greatly reduced in the hybrids with *gothica* parentage.

Sex ratios of broods from combinations of three of these species are shown in Table 1. Note that *gothica* parentage is nearly totally lethal for one sex, but that a substantial percentage of the deficient sex survives in hybrids with *zelicaon* mothers. Thus, the probability is greater than 95% that, in crosses with *polyxenes* males, the sex ratios of the two species are truly different.

Table 2 shows in sections *a* and *b* the fertility and hatchability of eggs of F_1 crosses between *P. gothica* and *P. zelicaon*. Section *c* shows fertility, as well as developmental viability of eggs, of these F_1 hybrids mated with 3 kinds of non-hybrid relatives. Control data from pure *gothica* and pure (but probably inbred) *zelicaon* appear in sections *d* and *e*. Egg fertility and hatchability of several other hybrid combinations involving *gothica* or *zelicaon* are given for comparison in sections *f* through *k*. At present this large body of data may appear more confusing than illuminating. But a few observations are appropriate. First, note that in general the various F_1 hybrid adults tended to exhibit high fertility, but their offspring showed low embryonic viability. The small brood 207A suggests that this tendency applies to F_1 *gothica* × *zelicaon*, and it will be of great interest to see whether it is confirmed in future backcrosses from such F_1 hybrids. Second, note that when non-hybrid females are mated to males of quite separate species, fertilizability and hatchability of eggs are commonly very high. Obviously, in studying hybrid fertility and viability it is essential to test the hybrids themselves, preferably by backcrossing.

Of several hundred larvae of *P. gothica* which my associates and I have reared, all were plain yellow in their subdorsal spotting; less than ten of these were from field-collected eggs or small larvae, the rest from about twenty confined wild-caught females. The

TABLE 1. Sex Ratios in *Papilio* F_1 Hybrids

A. Brood data.

Brood	Parentage	F_1 ♀♀	F_1 ♂♂	% ♀♀
#B-26(Ae)	♀ *gothica* × ♂ *polyxenes*	27	0	1.00
#411	♀ *zelicaon* × ♂ *polyxenes*	101	11	.90
#426	♀ *zelicaon* × ♂ *polyxenes*	8	6	.57
#10	♀ *polyxenes* × ♂ *gothica*	1	24	.04
#P-1-28(Ae)	♀ *polyxenes* × ♂ *gothica*	0*	23	.00
#115	♀ *polyxenes* × ♂ *zelicaon*	0	7	.00
#417	♀ *polyxenes* × ♂ *zelicaon*	0	3	.00

B. Ratio comparisons (♀♀ : ♂♂).

♀ *gothica* × ♂ *polyxenes*	27 : 0
♀ *zelicaon* × ♂ *polyxenes*	109 : 17
♀ *polyxenes* × ♂ *gothica*	1 : 47
♀ *polyxenes* × ♂ *zelicaon*	0 : 10

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* S. A. Ae obtained one intersex but no ♀♀ in this brood.

smaller number of *P. zelicaon* studied (perhaps forty from wild larvae and eggs and two or three hundred from about six captive females) showed polymorphism for this character, every sample of several larvae including yellow-spotted, pale-orange-spotted, and red-orange-spotted individuals. These are probably the phenotypes, respectively, of the *yellow* homozygote, the heterozygote, and the *red-orange* homozygote of two alleles at a single locus (see Clarke & Sheppard, 1956). I have found the same polymorphism in samples of wild larvae of *P. polyxenes* in Connecticut and Missouri. In *P. bairdii* in the San Bernardino Mountains of California and *P. machaon aliaska* Scudder in the Brooks Range of Alaska I have found only the red-orange phenotype. Thus, *P. gothica* is unusual in having *yellow* fixed in the known populations.

TABLE 2.

Egg Fertility and Embryonic Viability in Crosses of *Papilio gothica, P. zelicaon,* and Various Controls and Comparisons

Brood	Eggs laid	Colored (i.e., fertile)	Hatched
	a. *Papilio* F$_1$ ♀ *gothica* × ♂ *zelicaon*		
#723	22	7	1
#90	20	19	18
totals:	42	26	19
	colored/laid — .619	hatched/laid — .452	hatched/colored — .731
	b. *Papilio* F$_1$ ♀ *zelicaon* × ♂ *gothica*		
#721	431	428	384
#719	382	379	364
#744	306	287	254
#746	157	140	112
#743	122	108	85
#745A	110	109	97
totals:	1508	1451	1296
	colored/laid — .962	hatched/laid — .859	hatched/colored — .893
	c. Crosses including F$_1$ *gothica* × *zelicaon*		
	Papilio ♀ *zelicaon* × ♂ (F$_1$ ♀ *gothica* × ♂ *zelicaon*)		
#207A	25	21	9
	Papilio ♀ *machaon melitensis* × ♂ (F$_1$ ♀ *gothica* × ♂ *zelicaon*)		
#224A	34	34	25
	Papilio ♀ (F$_1$ ♀ *gothica* × ♂ *zelicaon*) × ♂ *kahli*		
#220A	39	?	36
	d. *Papilio gothica* — wild ♀♀ already fecundated		
#705	450	411	391
#704	293	274	256
#709A	217	197	186
#707	127	19	15
#699,701,708	131	122	107
totals:	1218	1023	955
	colored/laid — .840	hatched/laid — .784	hatched/colored — .934

TABLE 2 (continued)

Brood	Eggs laid	Colored (i.e., fertile)	Hatched
e. *Papilio zelicaon* — hand-paired (possibly sibs)			
#749	396	365	348
#750A	360	112	32
#713	375	331	207
totals:	1131	808	587
	colored/laid — .714	hatched/laid — .519	hatched/colored — .726
f. *Papilio* F_1 ♀ *polyxenes* × ♂ *gothica*			
#726	623	623	605
#700	280	241	234
#709B	61	59	56
totals:	964	923	895
	colored/laid — .957	hatched/laid — .928	hatched/colored — .970
g. *Papilio* F_1 ♀ *polyxenes* × ♂ *zelicaon*			
#736A	479	477	438
#735A	472	471	459
#734A	298	291	275
totals:	1244	1239	1172
	colored/laid — .996	hatched/laid — .942	hatched/colored — .946
h. *Papilio* F_1 ♀ *machaon* × ♂ *gothica*			
#732	452	437	396
#722	406	404	390
#730	358	356	329
#733	340	331	299
#731	126	122	115
totals:	1682	1650	1529
	colored/laid — .981	hatched/laid — .909	hatched/colored — .927

TABLE 2 (continued)

Brood	Eggs laid	Colored (i.e., fertile)	Hatched
i. *Papilio* F_1 ♀ *machaon* × ♂ *zelicaon*			
#757	398	391	384
#720	136	86	80
#758A	80	79	67
totals:	614	556	531
	colored/laid — .906	hatched/laid — .865	hatched/colored — .955
j. Crosses including F_1 *gothica* × *polyxenes*			
Papilio F_1 ♀ *gothica* × ♂ (F_1 ♀ *polyxenes* × ♂ *gothica*)			
#87	5	5	5
Papilio F_1 ♀ *kahli* × ♂ (F_1 ♀ *polyxenes* × ♂ *gothica*)			
#74	10	10	5
Papilio F_1 ♀ *polyxenes* × ♂ (F_1 ♀ *polyxenes* × ♂ *gothica*)			
#82	15	14	14
Papilio ♀ F_1 #82 × ♂ *gothica*			
#172	27	13	10
Papilio ♀ *zelicaon* × ♂ (F_1 ♀ *polyxenes* × ♂ *gothica*)			
#102	11	11	0
#117	12	11	5
Papilio ♀ *machaon melitensis* × ♂ (F_1 ♀ *polyxenes* × ♂ *gothica*)			
#81	15	15	15
k. Crosses including F_1 *zelicaon* × *polyxenes*			
Papilio ♀ (F_1 ♀ *zelicaon* × ♂ *polyxenes*) × ♂ *polyxenes*			
#413	70	67	55
Papilio ♀ (F_1 ♀ *zelicaon* × ♂ *polyxenes*) × ♂ *zelicaon*			
#418	93	90	?
Papilio ♀ *polyxenes* × ♂ (F_1 ♀ *polyxenes* × ♂ *zelicaon*)			
#240	62	?	7
Papilio ♀ (F_1 ♀ *zelicaon* × ♂ *polyxenes*) × ♂ *sib*			
#416	198	184	?
#420	41	41	?

Phenotypic Stability with Phyletic Divergence

It has been shown that extreme phenotypic similarity in wing and body characters has been retained in *Papilio gothica* and *zelicaon* while genotypic differences evolved in allopatry. Analogous findings have been reported for a wide scattering of animals and plants in which different demes look alike in one or more characters but hybridization reveals differences in the genotypic control of these characters. A recently reviewed example is that of certain poeciliid fishes, *Xiphophorus hellerii* and *X. montezumae,* in which the two parental species have the usual greenish wild-type Swordtail coloration, but the F_1 hybrids and offspring of repeated backcrosses to *hellerii* have the body bright red, sometimes with the caudal fin and its peduncle black (Kallman & Atz, 1966). This instance differs in detail from the *gothica—zelicaon* case in that F_1 hybrids between the two species of *Papilio* do not show major differences.

Various authors have discussed the adaptive significance of maintaining a constant phenotype despite substantial genotypic change. One mechanism for this homeostatic regulation has been called "canalization" by C. H. Waddington, a concept recently extended experimentally by Rendel (e.g., 1968) and others.

The extreme phenotypic similarity of many genetically well-differentiated pairs of species must be due to the maximal fitness associated with a stable phenotype. I consider it probable that a substantial percentage of "single species" of animals and plants presently well represented in taxonomic collections will prove to be a phenotypically stable group of two or more sibling species.

Helped by the refinements of their taxonomic procedures and the relative ease of culturing their breeding stocks, the drosophilists have long explored their species at this level of taxonomic sophistication. No other group has been so elegantly analyzed, although some advances in this direction have been made by chromosomal studies (e.g., *Erebia* and plebejine butterflies by Z. Lorkovic and H. de Lesse, grasshoppers by M. J. D. White, coccinellid beetles by S. G. Smith, and simuliid flies by K. H. Rothfels).

In some of these phenotypically stable clusters, whose siblings are not yet sympatric, the museum worker's "character displacement" may evolve when they eventually become partly sympatric. But I consider "displacement" unlikely in the hypothetically numerous instances in which the adaptiveness of phenotypic stability is not outweighed by the adaptive advantage of alteration of the *visual* phenotype to achieve the anti-hybridization and anti-competition sequelae to sympatry (see Remington, 1968, for formal discussion of the sequelae).

For several years I have had under study no fewer than three abundant "species" of butterflies in Connecticut and four in Colorado, each of which is probably a pair of widely sympatric and fully speciated entities. As with *Papilio gothica*, I have delayed formal naming of these species in the hope of finding recognition characters useful for determining museum specimens.

ACKNOWLEDGEMENTS

The day-to-day maintenance of the many laboratory broods required for this study has been carried out largely by several research assistants, Roger W. Pease Jr. during several seasons, and Orley R. Taylor Jr., Bruce Baker, and Eric E. Remington for shorter periods. These individuals, and most extensively Eric Remington, collected many of the wild specimens of *P. gothica*. James Scott provided the large sample from Jarre Canyon of the plains-edge deme. The late John C. Hopfinger, Richard Guppy, and Frank P. Sala sent breeding stocks of crucial *Papilio* from north-central Washington, Vancouver Island, and southern California. Christopher Henne, Charles N. Rudkin, and Fred T. Thorne kindly donated essential specimens of *P. rudkini*, and James Oberfoell went to special pains to collect for me a large series of the fascinating *polyxenes–machaon* taxa resident in the Dakotas. Dr. S. A. Ae kindly gave me relevant hybrid sex ratio data. Dr. Frederick H. Rindge of the American Museum of Natural History and Mr. Lloyd M. Martin of the Los Angeles County Museum have kindly guided me to the fine holdings of the *polyxenes–machaon* complex in their institutions. I have also studied important specimens in the collections of J. Donald Eff and G. R. DeFoliart, and especially the collection of P. Sheldon Remington now in the Peabody Museum. Thomas Brown prepared the excellent photographs. Essential support for various parts of this research was provided by National Science Foundation grants

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Literature Cited

Ae, S. A., 1965. A study of classification by interspecific hybridization in *Papilio.* Academia (Nanzan Univ.) **45-46**: 221-237.

Bauer, D. L., 1955. Notes on the *Papilio machaon* complex in Arizona. Lepid. News **9**: 7-10.

Brown, F. M., 1956. Colorado butterflies. Part IV. Pieridae, the whites and the sulphurs. Papilionidae, the swallowtails and parnassians. Denver Mus. Nat. Hist., Proc., **6**: 177-236.

Clark, A. H., 1932. The forms of the common Old World swallowtail butterfly *(Papilio machaon)* in North America, with descriptions of two new subspecies. U. S. Nat. Mus., Proc., **81**(11): 15 p., 8 pls.

——— 1936. The swallowtail butterflies. Smithsonian Rept. 1935: 383-408.

Clarke, C. A., and P. M. Sheppard, 1953. Further observations on hybrid swallowtails. Ent. Record Suppl. **65**(9): 12 p.

——— 1955. A preliminary report on the genetics of the *machaon* group of swallowtail butterflies. Evolution **9**: 182-201.

——— 1956. A further report on the genetics of the *machaon* group of swallowtail butterflies. Evolution **10**: 66-73.

Comstock, J. A., 1927. Butterflies of California. Comstock, Los Angeles. 334 p., 63 pls.

Coolidge, K. R., 1924. California butterfly notes — II. Brooklyn Ent. Soc. Bull. **19**: 44-47.

Edwards, W. H., 1895. Notes on collecting butterflies in western Colorado, with a particular account of certain papilios. Canad. Ent. **27**: 229-242.

Eller, K., 1936. Die Rassen von *Papilio machaon* L. Bayer. Akad. Wiss. math.-nat. Abt., Abh. n.F. **36**: 96 p., 16 pls.

Fischer, E., 1908. Neue Tagfalterformen meiner Sammlung. Societas Ent. **23**: 129-130.

Gunder, J. D., 1928. Additional transitional forms. Canad. Ent. **60**: 162-168, 2 pls.

Kallman, K. D., and J. D. Atz, 1966. Gene and chromosome homology in fishes of the genus *Xiphophorus.* Zoologica **51**: 107-135, 6 pls.

Langenheim, J. H., 1962. Vegetation and environmental patterns in the Crested Butte area, Gunnison County, Colorado. Ecol. Monogr. **32**: 249-285.

Maeki, K., and C. L. Remington, 1960. Studies of the chromosomes of North American Rhopalocera. I. Papilionidae. Lepid. Soc. Journ. **13**: 193-203.

Marr, J. W., 1961. Ecosystems of the east slope of the Front Range in Colorado. Univ. Colorado Studies (Biol.) **8**: 134 p.

Remington, C. L., 1956. Interspecific relationships of two rare swallowtail butterflies, *Papilio nitra* and *Papilio hudsonianus,* to other members of [the] *Papilio machaon* complex. Amer. Phil. Soc. Year Book 1955: 142-146.

——— 1958. Genetics of populations of Lepidoptera. Xth Int. Congress Ent. Proc. **2:** 787-805.

——— 1968. Suture-zones of hybrid interaction between recently joined biotas. Evol. Biol. **2:** 321-428.

Rendel, J. M., 1968. The control of developmental processes, p. 341-349. *In* E. Drake [ed.] Evolution and environment: a symposium presented on the occasion of the centennial of the foundation of the Peabody Museum of Natural History at Yale University. Yale Univ. Press, New Haven.

Ridgway, R., 1912 [1913]. Color standards and color nomenclature. Ridgway, Washington. 44 p., 53 pls.

Rothschild, W., and K. Jordan, 1906. A revision of the American papilios. Nov. Zool. **13:** 411-752.

Villalobos, C. and J., 1947. Atlas de los colores. El Ateneo, Buenos Aires. 88 p., 38 pls.

Wright, W. G., 1905. Butterflies of the West Coast. Whittaker and Ray, San Francisco. 257 p., 32 pls.